ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 38: 137–153 (2025)
DOI 10.3897/herpetozoa.38.e143411

Expanding habitat suitability under changing climate and land use may drive rapid expansion of Russell's viper (*Daboia russelii*) in Bangladesh

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https://zoobank.org/C6E28572-2060-4164-BE00-7EB3CF58FCE4

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Academic editor: Philipp Wagner ♦ **Received** 4 December 2024 ♦ **Accepted** 22 May 2025 ♦ **Published** 17 June 2025

Abstract

Eco-climatic and other environmental gradients significantly influence the geographic distribution of reptiles. In Bangladesh, the known range of Russell's viper (*Daboia russelii*) has expanded extensively in recent decades. Using species distribution modelling, we analysed habitat suitability, dispersal pathways, interspecific competition, and population dynamics to explore the drivers behind this phenomenon. Our findings indicate a five-fold increase in climatically suitable area (76,716 km²) since 2015, attributed to higher cold-season temperatures and increased dry-season precipitation, facilitating the viper's spread into previously unoccupied regions. The rapid dispersal of these snakes may have benefited from the strong currents of rivers, channels and seasonal waterways, and flat floodplain terrain. Additionally, the extension of agricultural and grassy habitats in new regions has provided abundant rodent prey and minimal predator or competitor pressures, creating ideal conditions for population growth. We also observed a female-biased population structure and large clutch sizes which may have further accelerated reproduction, contributed to rapid population expansion. In rural Bangladesh, where clinicians face multiple problems with the management of Russell's viper envenoming, increasingly frequent human encounters with this highly dangerous snake have caused great public concern. Despite the observed range expansion, the species also faces challenges such as unsuitable temperature fluctuations, reduced precipitation in some regions, and anthropogenic threats, including anti-snake attitudes and killings. Given the increasing risk of human-snake conflicts, implementing effective snakebite management plans and conservation strategies is crucial to safeguard public health while ensuring the survival of this ecologically and economically important predator of rodents.

Key Words

Eco-climatic parameters, female-dominant population, geospatial parameters, land use, range expansion, rice cultivation, river networks, snake, species distribution model, Viperidae

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Introduction

Russell's viper, *Daboia russelii* (Shaw & Nodder, 1797), is a medically important venomous snake species with a very wide geographic distribution in South Asia (Warrell and Williams 2023). This species belongs to the medically most significant snakes worldwide due to its common occurrence in agricultural lands, prompting frequent human encounters and snakebites, highly toxic and geographically variable venom, and complex syndrome of envenoming which is difficult to treat and results in severe morbidity with high rates of mortality and disability (Warrell 1989; Alirol et al. 2010; Pla et al. 2019; Senji Laxme et al. 2021). *Daboia russelii* has usually been reported as being wide-ranging across Pakistan, India, Sri Lanka, Bangladesh, Nepal, and Bhutan (e.g., Suraj et al. 2021), but the distributions of *D. russelii* and its Southeast and East Asian sister species *Daboia siamensis* (Smith, 1917) are actually patchy and discontinuous, suggesting important climatic and other environmental effects on the occurrence of these large vipers (Wüster 1998 , Warrell and Williams 2023). While a series of short snakebite case reports attributable to this species pointed to its presence in western and northern Bangladesh in the 1920s, no specimens or suspected or proven bites by *D. russelii* had been established to have occurred in this country until 2013 despite extensive efforts to find them (Banerji 1929; Kuch 2007; Amin et al. 2024a, b), suggesting that its populations in Bangladesh might have experienced declines in the late 20th century. As a result, *D. russelii* was assessed as Critically Endangered (CR) in 2000 (IUCN Bangladesh 2000). However, following its rediscovery in 2013 and 2014, a subsequent reassessment shifted the status of *D. russelii* to Near Threatened (NT) (Rahman 2015). In the following years, these vipers have been recorded from multiple additional localities and regions of Bangladesh, often in connection with claims by local peoples that such snakes had not been seen before in their areas, which suggests an ongoing range expansion (Ahsan and Saeed 2018; Haidar et al. 2023; Amin et al. 2024a, b). Initially documented in six administrative districts until 2015 (Rahman 2015), *D. russelii* has since been recorded in 27 out of 64 districts in Bangladesh (Amin et al. 2024 a, b). Over the same period, the number of snakebite incidents and deaths caused by this species has surged in Bangladesh (Haidar et al. 2023; Amin et al. 2024a, b), emphasising the need for additional research to investigate the dimensions and background of this public health emergency. Although several studies focusing on the biomedical aspects of *D. russelii* in Bangladesh have since been initiated, the ecological ramifications of its apparent expansion in this country have remained relatively unexplored.

Species distribution and range dynamics are heavily influenced by a species' acclimatisation potentiality, ecological preference, and environmental gradient (Wiles et al. 2003). In addition, range expansions may disrupt ecological equilibrium by increasing competition for ecosystem resources. Thus, understanding the ecological factors driving range expansion and population surges is essential for devising effective conservation and management strategies (Villero et al. 2017; Chowdhury et al. 2021). As a venomous snake species, *D. russelii* presents a dual challenge: Its range expansion not only raises public health concerns due to frequently severe and fatal envenoming (Senji Laxme et al. 2021) but also necessitates better knowledge of its ecological requirements and distribution to inform snakebite management policies.

Habitat suitability, determined by vegetation types (Rondinini et al. 2011), resource availability (Tschumi et al. 2020), and ecological services (López-López et al. 2007), plays a pivotal role in shaping species distribution (Muthoni et al. 2010). Anthropogenic activities, such as agricultural land use (Reverter et al. 2021), can profoundly alter these habitat characteristics (Bodo et al. 2021), impacting species presence (Pomara et al. 2014). Climate change further intensifies these pressures by altering habitat suitability (Archis et al. 2018; Zacarias and Loyola 2019), and associated ecological dynamics (Bastille-Rousseau et al. 2018), affecting species behaviour (Du et al. 2023), reproduction (Both and Visser 2001), and population trends (Pomara et al. 2014). In climate-vulnerable countries like Bangladesh (Harmeling 2008), these changes hold particular relevance for poikilothermic species like snakes (Chowdhury et al. 2022). Species distribution modelling has emerged as a powerful tool for investigating suitable niches (Hirzel et al. 2002; Mizsei et al. 2016, 2021) by considering various climate and geo-spatial variables. These statistically robust models allow us to predict the suitable habitat of a species for present, past, and future global scenarios (Jarvie and Svenning 2018; Park et al. 2022). Understanding the intricate relationships between snakes and eco-climatic and spatial factors is crucial for predicting species responses to environmental changes and their potential distribution.

Additionally, predator-prey relationships and interspecific competition are critical for regulating population dynamics and shaping community structures (Terborgh and Estes 2013; Mukherjee 2020). Predators act as population regulators, while competition influences species coexistence and resource partitioning (Pontarp and Petchey 2018; Radovics et al. 2023). Investigating the roles of predators and competitors in the habitats of *D. russelii* may provide insights into its apparent rapid range expansion in Bangladesh.

The country's subtropical environment, characterised by extensive floodplains and diverse habitats, supports rich biodiversity but also poses unique challenges. Frequent flooding (Kabir and Hossen 2019), facilitated by its low-lying topography and dense river networks (Khalid 2010), creates temporary aquatic corridors that enable the dispersal of species like *D. russelii* (Lesack and Marsh 2010). Snakes are known to disperse actively during flood events by leveraging their swimming abilities to move across flooded areas and explore and colonize new lentic habitats (Poiani 2006; Chowdhury et al. 2022). Moreover, agricultural fields provide ample prey, such as small mammals, and concealment in undergrowth

(Halstead et al. 2019), thus serving as prime habitats for many terrestrial venomous snakes including this viper (Warrell 1989; Glaudas 2021). Villagers are often encountering *D. russelii* while working in their agricultural fields, exacerbating human-snake conflict (Haidar et al. 2023; Amin et al. 2024a, b).

In this study, we employed species distribution modelling to evaluate the apparent rapid range expansion of *D. russelii* in Bangladesh. By predicting current and future climate suitability and analysing factors such as land use changes, predator-prey dynamics, and dispersal pathways, we aim to provide a comprehensive understanding of its ecological requirements. Our findings will support the development of effective conservation strategies and snakebite management plans, addressing both species preservation and public health concerns in Bangladesh and beyond.

Materials and methods

Study area

This study was conducted across the entire mainland of Bangladesh (Fig. 1B), situated between 23°41'N and 90°20'E, with a total land area of approximately 147,570 km^2 (Rashid 2019). Positioned at the confluence of the Indo-Himalayan and Indo-Chinese sub-regions within the Oriental biogeographic realm, Bangladesh serves as a critical corridor for species migration between the Indian subcontinent and Southeast Asia (Khan 2018). Its inclusion in the Indo-Burma biodiversity hotspot underscores its global ecological significance (Myers et al. 2000).

Bangladesh experiences a subtropical monsoon climate, marked by three distinct seasons: pre-monsoon (March-May), monsoon (June to October), and winter (November to February), with heavy rainfall dominating the monsoon period (Rashid 2019). Its landscape is predominantly shaped by the dynamic river systems of the Brahmaputra, Ganges (Padma), and Meghna, forming an extensive riverine and deltaic terrain (Sarker et al. 2016).

The ecological diversity of Bangladesh is reflected in its 12 bio-ecological zones (Nishat et al. 2002), seven climatic sub-regions (Rashid 2019; Chowdhury et al. 2022), and five distinct forest types, encompassing tropical and subtropical ecosystems (Henry et al. 2021). This combination of climatic variability and topographic complexity makes Bangladesh an ideal region for studying ecological processes and species distribution patterns.

Species occurrence data

A trained snake rescuer team has been actively rescuing *D. russelii* from the western regions of the country from 2019 to 2023 through a continuous field survey and responding to the rescue call. The specimens of *D. russelii* were collected randomly from various locations along with their habitat notes, highlighting its occurrence in previously unreported areas. We compiled a total of 231 occurrence points of *D. russelii* from three sources: field collections, research-grade database, and reliable print or electronic media (Fig. 1B). Between 2019 and 2022, 69 specimens were collected through active field work across various localities in Bangladesh under a permit from the Bangladesh Forest Department (permission letter no: 22.01.0000.101.23.2019.3173). These specimens are currently housed at the Venom Research Centre, Bangladesh, and were documented with detailed information, including collection date, geographical coordinates, sex, and morphological characteristics. To supplement this dataset, area of occupancy (AOO) polygons were obtained from the IUCN Red List assessment (Rahman 2015), and 100 random occurrence points were collected from these polygons. Additional verifiable data were obtained from global biodiversity repositories such as GBIF (GBIF Secretariat 2023) and iNaturalist (iNaturalist 2024). After rigorous validation and cross-referencing, we incorporated 62 occurrence points derived from literature, preserved specimens, and authenticated sources in print, electronic, and social media.

Variables for suitable niche analysis

We obtained 19 bioclimatic variables from WorldClim 2.0 at a spatial resolution of 30 arc-seconds (approximately 1 km^2 grid cells) for both current (1970–2000) and future (2061–2080) climate scenarios (Hijmans et al. 2005). To ensure consistency and minimise biases due to varying measurement scales, all variables were standardised using z-score transformation. Highly correlated variables (correlation coefficient, $r > 0.9$) were excluded to address multicollinearity concerns (De Marco and Nóbrega 2018), resulting in a final selection of 12 bioclimatic variables (Table 1). Future climate suitability for *D. russelii* was modelled using 23 climate projections for 2080 based on the shared socioeconomic pathway 370 (ssp370) scenario (Masson-Delmotte et al. 2021). All vector and raster datasets were prepared within the WGS84 coordinate system and clipped to match Bangladesh's geographical boundaries.

In addition, seven spatial variables (e.g., bio-ecological zones, climatic sub-regions, elevation, flood plains, forest types, land use, and river zones) were included in the analysis (Table 1). These datasets were converted into raster format following the methodologies by Chowdhury et al. (2022) and Dutta et al. (2024). Autocorrelation tests confirmed that the spatial variables were independent. The 12 bio-ecological sub-zones and seven climatic sub-regions were digitised from published literature (Nishat et al. 2002; Rashid 2019). Floodplain and river zone data were sourced from the Bangladesh Agricultural Research Council (Bangladesh Agricultural Research Council 2019) and the Water Development Board, as cited by Sarker et al. (2016).

Table 1. Twelve bioclimatic and seven spatial variables used in this study.

No.	Variable Name	Description	Category
1	Bioclim 1	Annual mean temperature (°C)	Temperature
2	Bioclim 2	Mean diurnal range (mean of monthly (max temp.-min temp.))	
3	Bioclim 3	Isothermality (Bio02/Bio07) × 100	
4	Bioclim 4	Temperature seasonality (standard deviation × 100)	
5	Bioclim 5	Max. temperature of warmest month (°C)	
6	Bioclim 6	Min. temperature of coldest month (°C)	
7	Bioclim 7	Temperature annual range (Bio05-Bio06) (°C)	
8	Bioclim 12	Annual precipitation (mm)	Precipitation
9	Bioclim 14	Precipitation of driest month (mm)	
10	Bioclim 15	Precipitation seasonality (coefficient of variation)	
11	Bioclim 17	Precipitation of driest quarter (mm)	
12	Bioclim 18	Precipitation of warmest quarter (mm)	
13	Spatial 1	Elevation	Topography
14	Spatial 2	Bio-ecological zones	Ecological
15	Spatial 3	Climatic sub-regions	Climate
16	Spatial 4	Flood plain	Hydrological
17	Spatial 5	Forest types	Ecological
18	Spatial 6	Land use	Land use
19	Spatial 7	River zones	Hydrological

Elevation data were collected from the Earth Resources Observation and Science Centre using SRTM 3 arc-second (90 × 90 m^2) datasets (United States Geological Survey 2019). Land use and land cover data, with a spatial resolution of 100 × 100 m^2, were obtained from the Copernicus Global Land Service (Buchhorn et al. 2019). Forest cover data, at a resolution of 30 × 30 m^2, were acquired from the Bangladesh Forest Department repository (Henry et al. 2021). All raster datasets were resampled to a standard resolution of 1 km^2 using the nearest neighbour resampling technique in the ArcGIS environment. These datasets featured categorical pixel values to represent distinct environmental attributes. For example, the flood raster categorised pixels as either outside the flood zone (value = 1) or within it (value = 2). Similarly, five other variables—bio-ecological zones, climatic sub-regions, forest zones, land use, and river zones—had complex categorical structures, with varying numbers of categories per raster file. This categorisation provided a detailed representation of the environmental characteristics across the study area, supporting comprehensive ecological analyses.

The spatial and temporal dispersion patterns of *D. russelii* were analysed using 69 field-collected occurrence records. To evaluate yearly range expansion, the occurrence data were organised chronologically and visualised using ArcGIS. Each record was sorted by year and mapped at the district level, with newly recorded districts added incrementally for each subsequent year. This stepwise approach enabled a progressive mapping of the viper's distribution across Bangladesh over time. By examining the assumed yearwise distributional changes, potential routes of dispersion were inferred. This provided insights into possible geographic pathways and expansion trends of *D. russelii*, highlighting areas of recent colonisation and facilitating the identification of ecological factors driving this expansion.

Species distribution model

To predict the suitable climatic niches of *D. russelii* in Bangladesh, we utilised Species Distribution Modelling (SDM) following the methodology described by Rangel and Loyola (2012). Initially, the six distinct spatial variables with categorical values—bio-ecological zones, climatic sub-regions, flood plain, forest types, land use, and river zones—were converted to raster with continuous values. This was done by calculating the proportion of the area of each category under the species' Area of Occupancy (AOO). First, each categorical raster was masked using the AOO of this viper, retaining the number of categorical cells within the species' AOO. The proportion of the AOO area within each category was then calculated to produce a category-specific percent occupancy. The percent occupancy values were then used to reclassify the categories by replacing each category value with the corresponding percent occupancy. For example, if the AOO of this viper species distributed 40% over the cells of category A and 60% over the cells of category B of a spatial raster, we assigned 0.4 to all cells of category A and 0.6 to all cells of category B. The rest of the cell of that raster was assigned as 0. Finally, raster stack of 19 variables (Table 1) were used to perform the species distribution model.

We employed the *Bioclim*() and the Maximum Entropy *Maxent*() algorithms to determine the suitable climate space for *D. russelii* in Bangladesh. The *Bioclim*() is a simple and non-parametric approach suitable for predicting climate-driven niches (Beaumont et al. 2005; Hallgren et al. 2019), while the *Maxent*() model is a machine-learning algorithm to determine the suitable climate space for *D. russelii* in Bangladesh (Phillips 2021). We used the 'DISMO' (Hijmans et al. 2017) and 'RJAVA' (Urbanek 2024), 'MAXNET' (Phillips 2021) packages on R platform (version 4.4.1) with the integration of several supporting packages, including 'RASTER' (Hijmans and Van Etten 2019), 'MAPTOOL' (Bivand et al. 2016), 'RGDAL' (Bivand et al. 2019), 'SP' (Pebesma and Bivand 2019) and 'SF' (Pebesma 2018). This approach provided a robust framework for identifying potential climate-driven habitats of *D. russelii*, facilitating further analysis of its distribution dynamics across Bangladesh. To ensure transparency, reproducibility, and comprehensive documentation of the species distribution modelling process, we followed the ODMAP (Overview, Data, Model, Assessment, and Prediction) protocol (Zurell et al. 2020). ODMAP provides a standardised framework for documenting each step of the modelling workflow, from data collection and pre-processing to model development, evaluation, and prediction. By adopting this structured approach, we aimed to enhance the clarity of our methodological decisions and facilitate future replication

or extension of our study (Suppl. material 2). The models were evaluated using the area under curve (AUC), threshold-dependent sensitivity, specificity, and Cohen's Kappa.

Suitable and unsuitable area analysis

For this analysis, we first reclassified the predicted raster outputs from both the Bioclim and Maxent models using their respective threshold values. Cells with values above the threshold were assigned a value of 1 (indicating suitable areas), while cells with values below the threshold were assigned 0 (indicating unsuitable areas). These reclassified raster files were then ensembled. Since Maxent provided more realistic predictions with higher and more consistent AUCs for both current and future climate scenarios, it was assigned a higher weight in the ensemble operation. The ensemble formula was as follows:

$$\text{Ensembled}_{(\text{current/future})} = (0.3 \times \text{reclassified Bioclim}_{(\text{current/future})}) + (0.7 \times \text{reclassified Maxent}_{(\text{current/future})})$$

The resulting ensembled raster was then reclassified into three distinct categories to indicate climatic suitability. To determine the threshold, we multiplied the threshold values from each model by their respective weights. For example, the threshold probability for the Bioclim prediction in the current climate is 0.0022, and for Maxent, it is 0.1356. Thus, the weighted threshold for the current climate is: $(0.3 \times 0.0022) + (0.7 \times 0.1356) = 0.09558$.

This weighted threshold was used to reclassify the ensembled predictions into three categories:

- Cells with no occurrence probability were assigned a value of 0.
- Cells with probability values from $-\infty$ to 0.09558 were classified as 1 (unsuitable areas).
- Cells with probability values greater than 0.09558 were classified as 2 (suitable areas).

A similar process was applied to future climate model predictions, where the following categories were used:

- Cells with no occurrence probability were assigned a value of 0.
- Cells with probability values from $-\infty$ to 0.03984 were classified as 3 (unsuitable areas).
- Cells with probability values greater than 0.03984 were classified as 6 (suitable areas).

This reclassification enabled a clear categorization of each cell within the raster for both the current and future climate conditions. To facilitate direct comparison between current and future suitability, we then overlapped the raster files from both time periods and summed the corresponding cell values to generate distinct integer values, as follows:

	Future unsuitable (3)	**Future suitable (6)**
Currently unsuitable (1)	1+3 = 4 (Common unsuitable)	1+6 = 7 (Currently unsuitable, future suitable)
Currently suitable (2)	2+3 = 5 (Currently suitable, future unsuitable)	2+6 = 8 (Common suitable)

Principal component analysis for identifying influential climatic factors

To identify the key factors influencing the distribution of *D. russelii* in Bangladesh, we performed a Principal Component Analysis (PCA) using SPSS, following the methodology described by McGarigal et al. (2000). PCA is a robust statistical tool that reduces dimensionality by identifying the most important variables that account for the maximum variance in a dataset. This allows us to isolate the climatic factors that most significantly drive the species' distribution (Bueno de Mesquita et al. 2021; Joswig et al. 2022). Data were collected for 13 predictor variables, including 12 bioclimatic variables and elevation, at the occurrence points of *D. russelii*. Additionally, six spatial variables were converted from categorical to continuous format by calculating the percentage occupancy of each category within the species' known range in Bangladesh. This transformation ensured consistency across variables, enabling a more accurate PCA. The results of the PCA highlighted the relative importance of climatic and environmental variables, providing valuable insights into the ecological drivers of the distribution of *D. russelii* and guiding subsequent habitat modelling efforts.

Sex ratio analysis

From 2019 to 2022, 61 vipers were collected during fieldwork and through rescue operations. Their sexes were determined using sex determination probes following established methodologies (Marais 1984; Mader 2006). This analysis aimed to evaluate the population's sex ratio and its demographic structure over multiple years. However, data from 2022 and 2023 were excluded from the analysis due to incomplete records. By determining the sex ratio, we gained insights into the population dynamics of *D. russelii*, which could have implications for understanding its reproductive ecology.

Analysis of predators, competitors, habitat, and annual floods

Animals known to prey on snakes were identified as potential predators of *D. russelii*. Information on the conservation status and population trends of these predators (Suppl. material 3) was sourced from published literature, including the Red List of Bangladesh Volumes 2, 3, and 4 (IUCN Bangladesh 2015 a, b, c). Similarly, potential competitor species were identified based on their dietary overlap and shared habitat preferences with *D. russelii* (Suppl. material 4).

Data on these possible competitors were gathered by analysing their feeding habits, behaviours, and geographic distributions as described in the same literature sources.

To assess habitat conditions, data on rice production and paddy fields, which serve as primary habitats for *D. russelii*, were collected from the Yearbook of Agricultural Statistics (Bangladesh Bureau of Statistics 2023) spanning the years 2012 to 2022. Additionally, information on annual floods, a key factor influencing snake dispersal and habitat dynamics, was extracted from the Annual Flood Report 2021 published by the Bangladesh Water Development Board (Barua et al. 2021). This multi-faceted approach enabled a comprehensive understanding of the ecological factors influencing the expansion and population trends of *D. russelii*, providing insights into its interactions with predators, competitors, and its flood-prone habitat.

Data resources

The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, and are available at https://ipt.pensoft.net/resource?r=russells_viper_bangladesh.

Results

Pattern of dispersion

Our field observation found that *D. russelii* might be dispersed through two possible ways—one exploiting aquatic channels and the other relying on terrestrial plains—enabling the species to expand its range across previously unoccupied habitats. As of 2019, the species' distribution was primarily concentrated in the north-western regions of Bangladesh along the Padma and upper Meghna Rivers (Fig. 2A). From 2019 to 2021, dispersion was observed through riverine channels, where individuals moved from the upper to the lower Meghna River (Fig. 2B, C). This pathway might enable the viper to colonise new riverside localities, including tidal floodplains and coastal islands within the Bay of Bengal. On the other hand, sightings recorded in previously unoccupied localities such as Meherpur, Jhenaidah, and Chuadanga by 2022 can be deduced as terrestrial dispersion (Fig. 2D). By 2023, *D. russelii* had reached Satkhira, a coastal district in southwestern Bangladesh, through terrestrial corridors that included crossings via Jashore district (Fig. 2E).

Current and future suitable climate spaces

Climate model analysis revealed that *D. russelii* currently has a broad suitable climatic area of approximately 76,716 km² in western Bangladesh (Fig. 3A, B). However, projections for 2080 indicate a slight reduction in this suitable space for this viper. Across both present and future scenarios, approximately 75% of the study area remains unsuitable for *D. russelii* (Fig. 4).

Currently, the estimated suitable climate space (Fig. 3A, B) is nearly five times larger than the species' observed area of occurrence (AOO: 14,344 km²). These areas are predominantly located along major river systems, including the Padma, Meghna, and Jamuna, and encompass regular floodplains, low tidal plains, and diverse forest types such as tropical deciduous, mangrove, and village forests.

The current suitable climate space of *D. russelii* in Bangladesh is confined to the western half of the country. According to the weighted ensemble of predicted models (Maxent and Bioclim), the major portion of the suitable space is situated at the banks and char lands of the Padma, Meghna, and the Jamuna River. Most of these areas are riverbanks, and lower flat plains, and cover the major portion of the village forest of the southern, central, north-west and northern part of the country.

The river bank area of the north-west and central parts is the most suitable place for this viper ($p > 0.6$) under the current climate scenario (Fig. 3A), but its suitability is slightly reduced in 2080 ($p < 0.4$) (Fig. 3B). The southern coastal area and the mangrove forest also provide current suitable space ($0.4 > p < 0.6$), but reduced in the future ($p < 0.2$) (Fig. 3A, B).

Both Bioclim and Maxent models strongly support that the riverbank, char lands, and lower floodplains of Padma, Meghna and Jamuna rivers of the country provide the current suitable climatic condition for *D. russelii* in Bangladesh ($p > 0.8$ for Maxent, 0.5 for Bioclim). In the future (2080), this suitable climate situation slightly decreases ($p \leq 0.005$ for Bioclim and $p \leq 0.5$ for Maxent) (see details in Suppl. material 5).

Model evaluation

The Bioclim model proved to be highly effective in the current climatic condition, with high discriminatory power (AUC = 0.9851), in addition to high sensitivity (0.9821) and specificity (0.9739), thus indicating its ability to correctly differentiate between suitable and unsuitable climate space. However, its performance significantly declined when tested against future climate scenarios (AUC = 0.6512), as indicated by the low specificity (0.3087) and low Kappa value (0.3054) (Table 2).

In contrast, the Maxent model showed consistently strong performance in both the current and future contexts, as evidenced by consistent AUC values (0.9730 for the present context and 0.9718 for the future context), maximum sensitivity (1.0), and high specificity (0.9522) in both cases. This highlights the ability of Maxent to clarify complex environmental interactions and its resilience to changing climatic conditions, thus making it a more

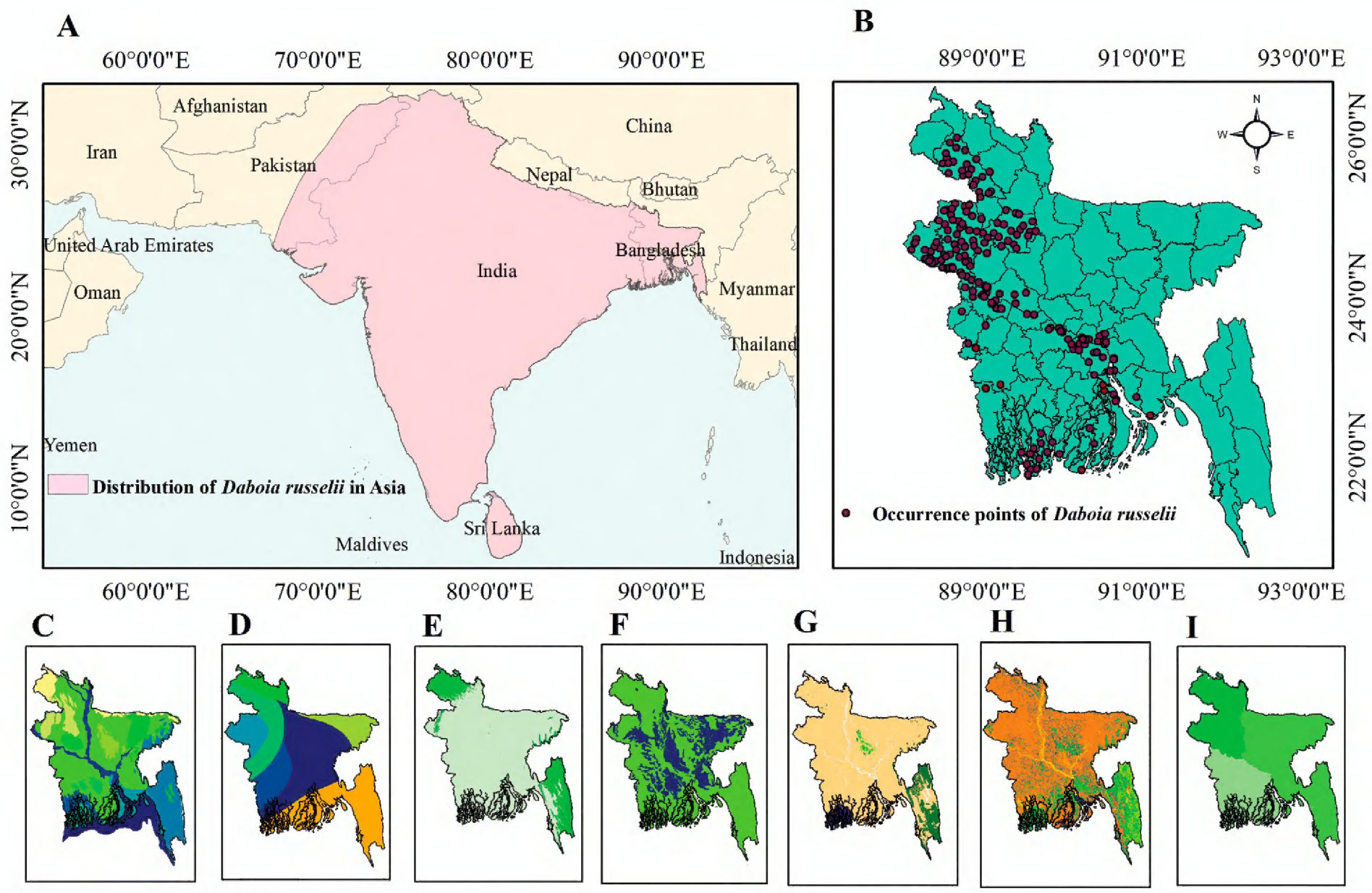

Figure 1. A. Distribution of *Daboia russelii* in Asia (Suraj et al. 2021); **B.** Occurrence points of *D. russelii* used for species distribution modelling; **C.** 12 bio-ecological zones (Nishat et al. 2002); **D.** Seven climatic sub-regions (Rashid 2019); **E.** Elevation (United States Geological Survey 2019); **F.** Flood plain (Bangladesh Agricultural Research Council 2019); **G.** Forest zones (Henry et al. 2021); **H.** Land use types (Buchhorn et al. 2019); **I.** River zones (Sarker et al. 2016). The details of the seven spatial variables are provided as Supplementary material 1.

Table 2. Comparative performance evaluation of Bioclim and Maxent models in predicting the potential distribution of *Daboia russelii* under current and future (2080) scenarios in Bangladesh.

Model	AUC	Threshold	Sensitivity	Specificity	Kappa
Bioclim (Current)	0.9851	0.0022	0.9821	0.9739	0.9558
Bioclim (Future)	0.6512	0.0005	1	0.3087	0.3054
Maxent (Current)	0.9730	0.1356	1	0.9522	0.9515
Maxent (Future)	0.9718	0.0567	1	0.9522	0.9515

reliable tool for predicting the distribution of *D. russelii* in future contexts (Table 2).

The SDM analysis for *D. russelii* in Bangladesh shows that 23% of the country's land is climatically suitable, while 77% is unsuitable. Future projections reveal that 21% of the land will be suitable, compared to 79% that will remain unsuitable. The areas found to be suitable in the current and future evaluations include 19%, while 76% of the country is unsuitable in both temporal analyses. Additionally, about 4% of the currently suitable areas are expected to shift to an unsuitable category, while about 1% of the areas found to be unsuitable will be suitable in the future (Fig. 4).

Despite these changes, the regular floodplain remains a consistent feature within both present and future suitable climatic spaces, underscoring its importance as a stable habitat component for *D. russelii* in Bangladesh.

Responsible climatic and spatial variables to outline suitable climate spaces

Principal Component Analysis (PCA) underscored the complex interplay of climatic and spatial factors driving the distribution and habitat suitability of *D. russelii* in Bangladesh. It identified three components (PC1, PC2, and PC3) that collectively explained over 79% of the variance in the occurrence of *D. russelii*. These components encompassed 15 significant variables (loading value > 0.7), which either positively or negatively influence the species distribution (Table 3).

PC1 accounted for the largest variance and highlighted key variables influencing the species distribution. Positive contributors included minimum temperature of the coldest

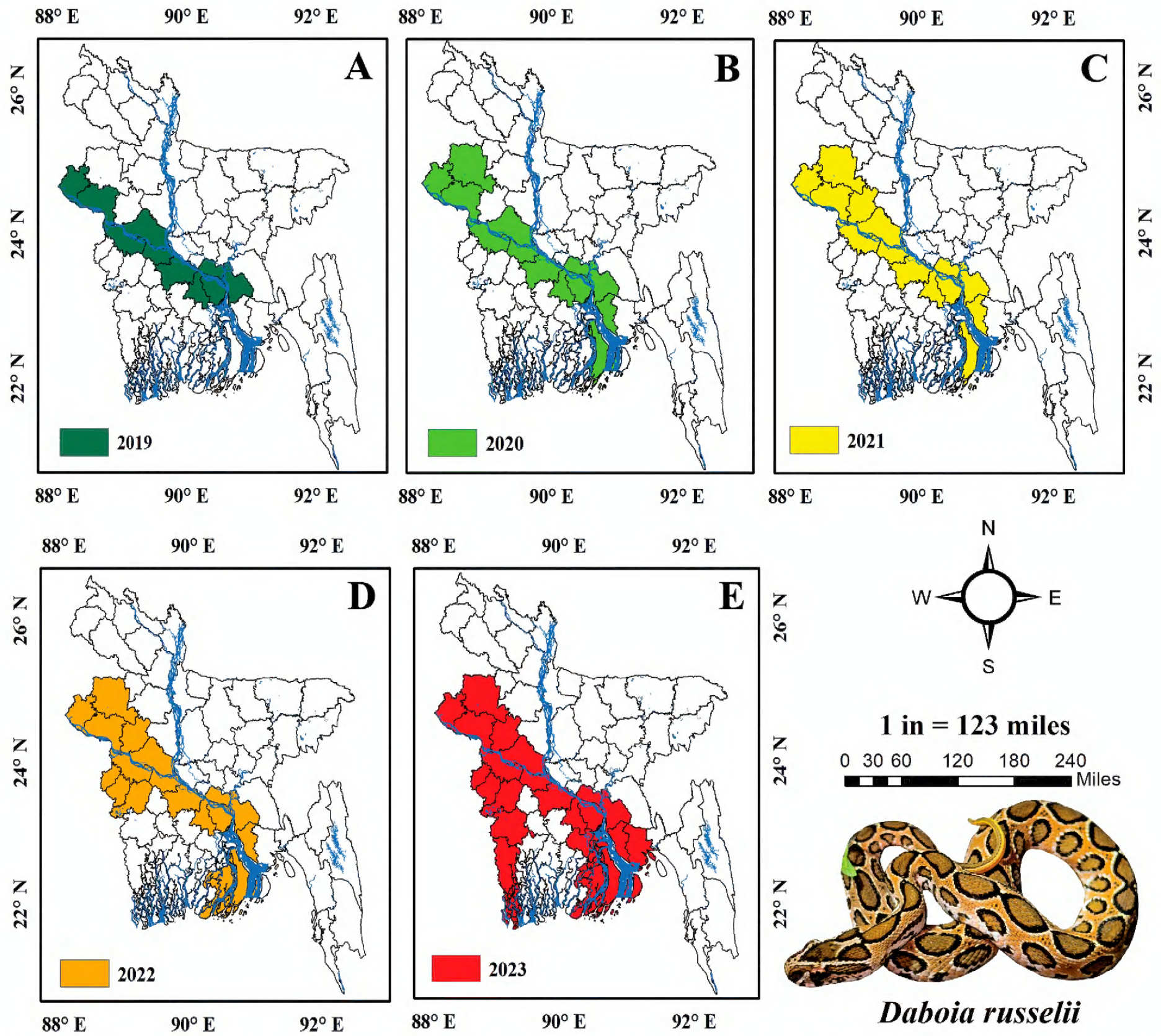

Figure 2. Occurrence records of *Daboia russelii* in new localities in Bangladesh, illustrating its dispersal pattern: **A.** In 2019; **B.** 2020; and in **C.** 2021, this species was observed along the riverine channels of the Padma and Meghna Rivers; **D.** Since 2022, this species has occurred in new localities independent of river channels; **E.** In 2023, the species had reached coastal districts in the southwestern region of the country.

month (0.937), annual precipitation (0.805), precipitation of the driest month (0.942), and precipitation of the driest quarter (0.905). Conversely, variables with negative influences included mean diurnal range (-0.941), temperature seasonality (-0.920), temperature annual range (-0.868), and elevation (-0.724). PC2 identified additional variables affecting the distribution of *D. russelii*. Positively associated factors were annual mean temperature (0.725) and maximum temperature of the warmest month (0.722). In contrast, negative influences came from isothermality (-0.737) and precipitation of the warmest quarter (-0.935).

Sex-based population structure

Over a four-year study period, the collected individuals of *D. russelii* exhibited a distinct female-biased trend (Fig. 5). The trend lines in Fig. 5 further support this observation, showing an upward trajectory for females and a corresponding decline in males. The high coefficient of determination ($R^2 = 0.98$) for both male and female trends suggest a strong, consistent pattern in the sex ratio dynamics over the analysed period. In 2019, the sex ratio of collected specimens was balanced at 1:1, indicating equal male and female representation. By 2020, females began to outnumber males with a ratio of 1:1.3, reflecting an increase in the female proportion to approximately 56.5% of the sample. This female dominance became more pronounced in 2021, with females accounting for 66.7% of the population and a sex ratio of 1:2 favouring females.

Role of predators and competitors in population expansion

The apparent population expansion of *D. russelii* in Bangladesh may also be influenced by a significant decline in both its predators and competitors. Specifically,

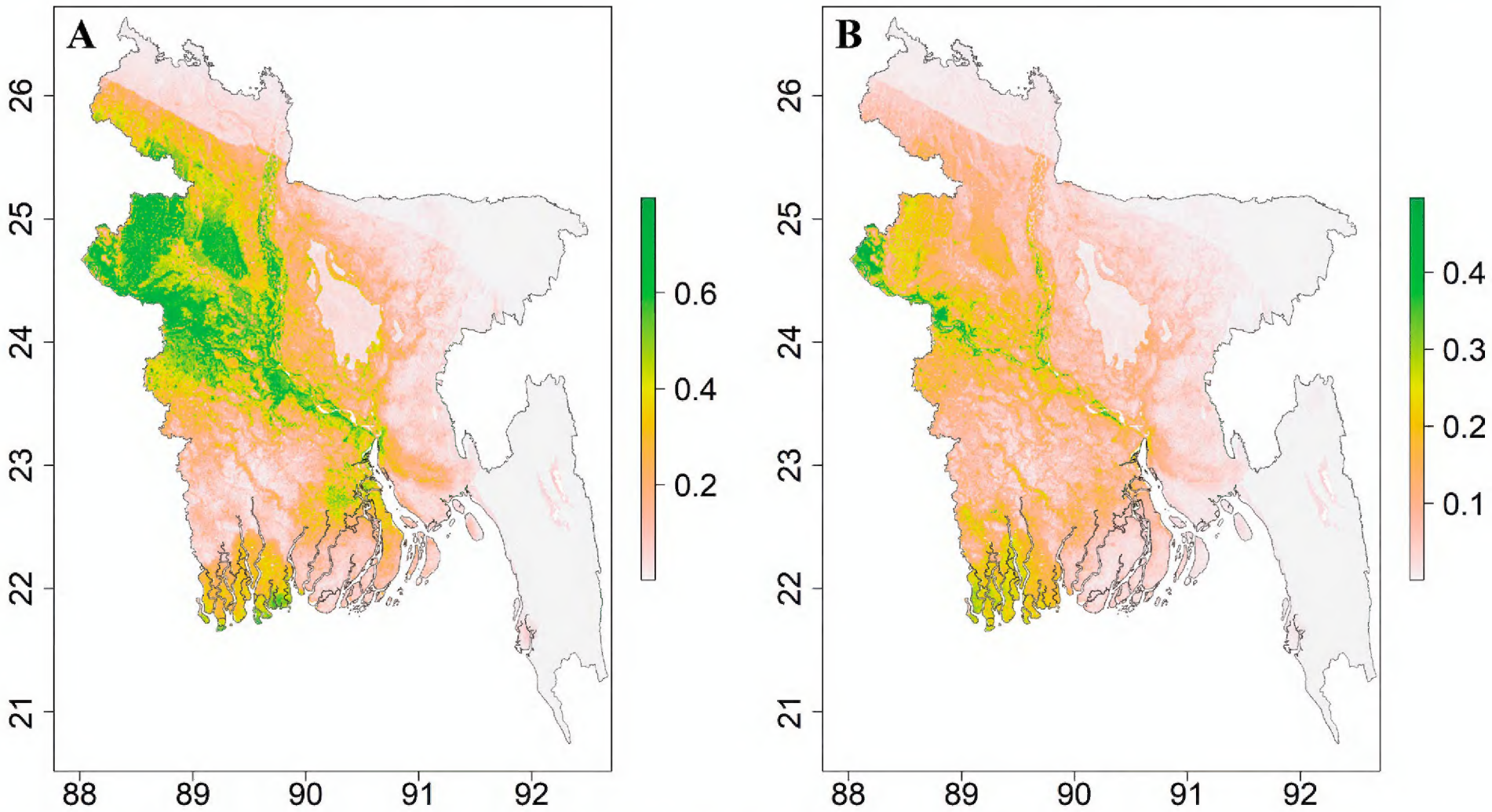

Figure 3. Suitable climate map of *D. russelii* in Bangladesh. **A.** Weighted present suitable climate space (0.7*Maxent current) + (0.3* Bioclim current). **B.** Weighted future (2080) suitable climate area (0.7*Maxent future) + (0.3* Bioclim future).

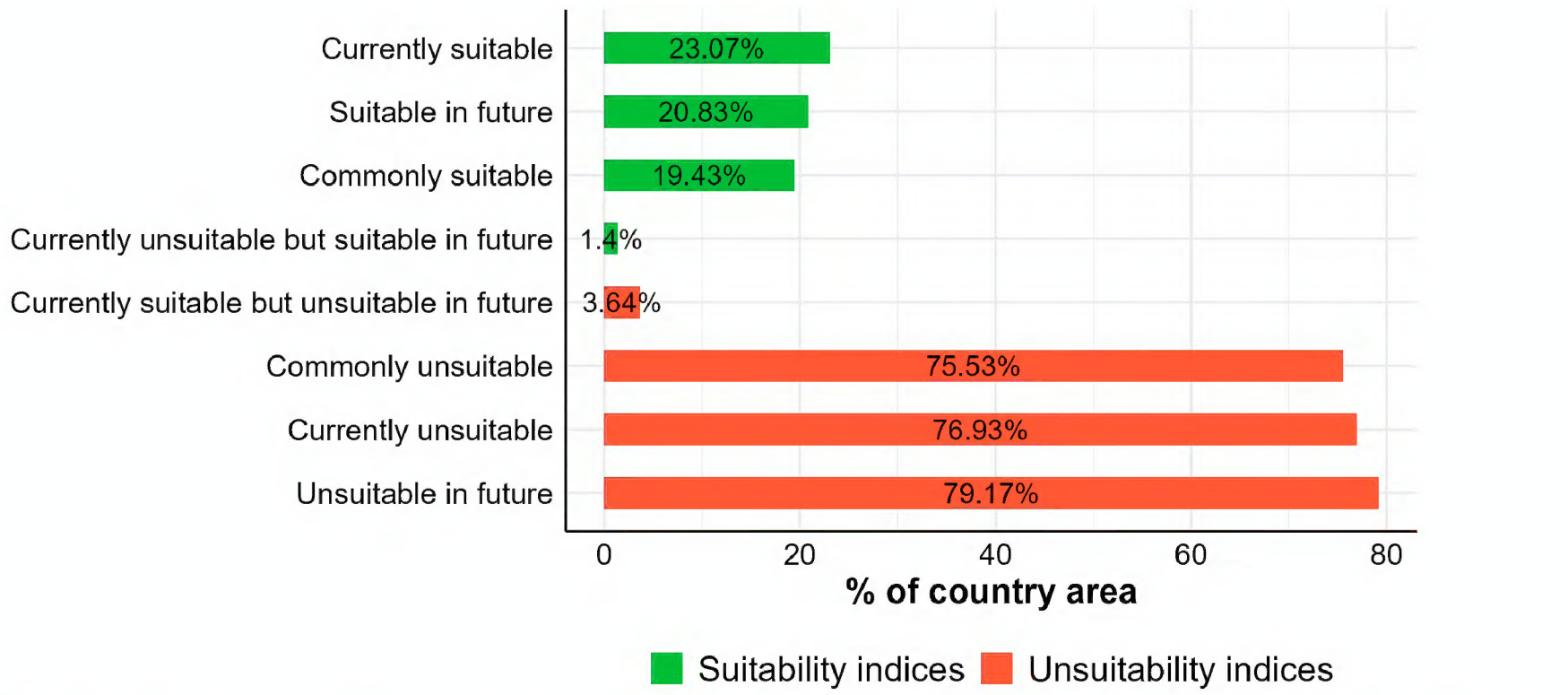

Figure 4. Suitability index based on weighted average ensemble of Bioclim and Maxent for present and future climate areas (0.7 * Maxent) + (0.3 * Bioclim) shows that currently 23% of the area are suitable and the remaining 77% unsuitable for *Daboia russelii* in Bangladesh. In the future, 79% of the country area is suspected to be climatically unsuitable.

the population of predators has declined by 29%, while competitors have seen a more substantial decline of 46% (Fig. 6A, B). Notably, the status of many species remains uncertain, with 36% of predators and 32% of competitors categorized as "unknown" according to IUCN (2015).

Conversely, only a small proportion of species—4% of predators and 1% of competitors—have shown an increasing population trend. Threat levels are also concerning, with approximately 14% of predators and 11% of competitors regionally classified as threatened or near-threatened (CR, EN, VU) by IUCN Bangladesh (2015) (Fig. 6C, D). Additionally, 18% of predators and 19% of competitors are classified as Near Threatened (NT) due to declining population trends.

Role of land use type in habitat selection

The analysis of habitat selection based on land use indicates a pronounced trend toward increasing rice cultivation over the past two decades. Specifically, gross rice production has shown a rapid increase with a strong correlation ($R^2 = 0.93$) between time and production trends (Fig. 6E). Between the fiscal years 2001-02 and 2021-22, the cultivated area dedicated to rice expanded modestly by 0.49%, while total rice production surged by 2.32%. This reflects an intensification of agricultural practices, likely driven by higher yields per year rather than a significant expansion in cultivated area. Greater and more frequent

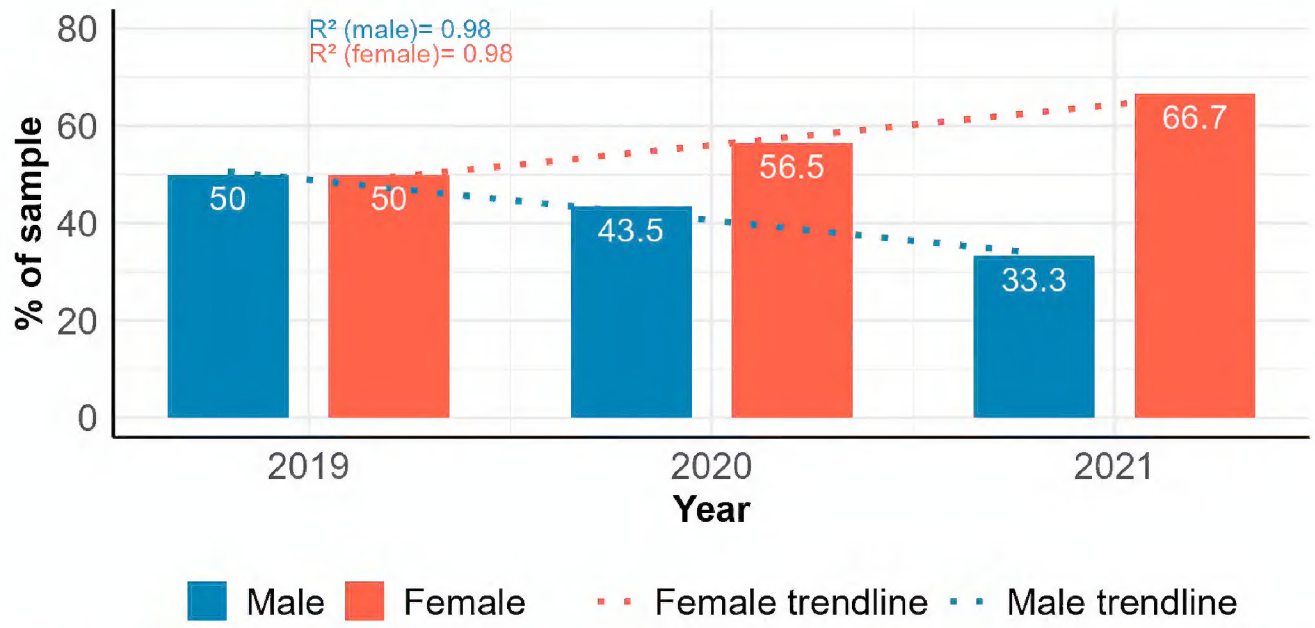

Figure 5. Sex-based population structure of *Daboia russelii* collected in Bangladesh from 2019 to 2021 suggests a gradual increase in females in natural habitats.

Table 3. Loading scores of different variables in Principle Component Analysis (PCA).

Variable Name	Description	PC1	PC2	PC3
Bioclim 1	Annual mean temperature	0.592	0.725	0.022
Bioclim 2	Mean diurnal range	-0.941	0.269	-0.051
Bioclim 3	Isothermality	-0.406	-0.737	-0.227
Bioclim 4	Temperature seasonality	-0.920	0.315	0.090
Bioclim 5	Max. temperature of warmest month	-0.670	0.722	0.039
Bioclim 6	Min. temperature of coldest month	0.937	-0.034	0.066
Bioclim 7	Temperature annual range	-0.868	0.467	-0.007
Bioclim 12	Annual precipitation	0.805	-0.482	-0.027
Bioclim 14	Precipitation of driest month	0.942	-0.079	0.077
Bioclim 15	Precipitation seasonality	-0.570	-0.255	0.700
Bioclim 17	Precipitation of driest quarter	0.905	0.315	0.001
Bioclim 18	Precipitation of warmest quarter	0.087	-0.935	-0.114
Spatial 1	Elevation	-0.724	-0.356	0.386
Spatial 2	Bio-ecological zones	0.492	0.421	-0.197
Spatial 3	Climatic sub-regions	-0.103	0.073	-0.854
Spatial 4	Flood plain	0.115	-0.063	-0.498
Spatial 5	Forest types	0.566	0.079	0.690
Spatial 6	Land use	0.643	0.174	0.417
Spatial 7	River zones	-0.726	-0.335	0.094

availability of rice, for example, due to multiple planting and harvest cycles per year, is expected to result in higher rodent populations which in turn could sustain higher populations of rodent-eating snakes like *D. russelii*.

Role of flooded areas in dispersal

Over the last two decades, Bangladesh has shown an increasing trend in flood-affected lowland areas (Fig. 6F). Notably, major flood events in 2004, 2007, 2017, and 2020 impacted 38%, 42%, 42%, and 40% of the country's total area, respectively. These data indicate a consistent rise in the extent of flood-affected regions. Floods can facilitate the terrestrial species over the inundated landscape.

Discussion

Our study confirms a synergistic effect of several climatic and spatial variables on the geographic expansion of *Daboia russelii* in Bangladesh, with a female-biased population structure. The IUCN Red List assessment has documented an increasing distribution trend of this viper in 2015 (IUCN Bangladesh 2000; Rahman 2015). Our species distribution models revealed that the realised climatically suitable areas are four times larger than the observed ranges in 2015 (Rahman 2015). So, these suitable climate spaces that exist beyond the currently observed distribution of this viper may provide potential for further dispersion into suitable climatic zones in the near future as suitable climate significantly influences snake populations and their distribution (Muthoni et al. 2010; Archis et al. 2018; Chowdhury et al. 2022). Being a proficient swimmer, *D. russelii* is capable of travelling long distances using water currents and floating debris through river channels (Warrell 1989), which is predominantly effective in riverine Bangladesh. In addition, floodwaters in this flood-prone country create temporary connections between lentic and lotic water bodies, notably facilitating dispersal pathways for good swimmers like *D. russelii* to move across flooded areas and explore new habitats (Lesack and Marsh 2010). In addition, there are no high-elevation geographical barriers between the

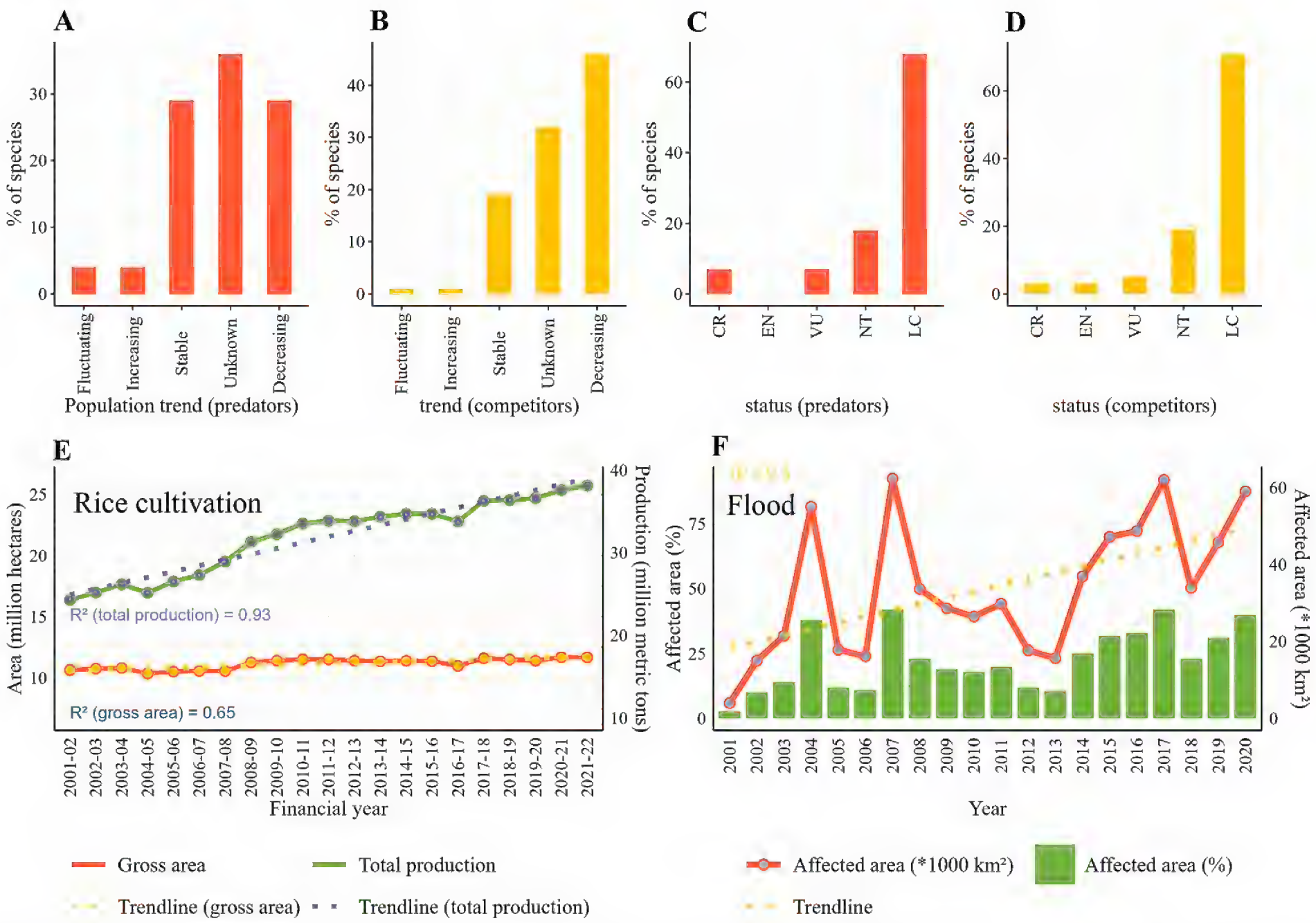

Figure 6. Decreasing population trends of potential predators (**A**) and competitors (**B**) might facilitate population expansion of *Daboia russelii*. A total of 32% of potential predators (**C**) and 30% of potential competitors (**D**) were assessed under threatened or near threatened categories regionally by IUCN Bangladesh in 2015. Lists of potential predators and competitors of *D. russelii* with their population trends and status are provided in Supplementary material 3 and 4, respectively. **E.** Increasing trends of land use for rice cultivation and gross production of rice over the years in Bangladesh (2001-02 to 2021-22) provided additional paddy field habitat for *D. russelii* and more food for their rodent prey. **F.** Flood affected areas in Bangladesh over the last 20 years (2001-2020) might provide dispersal pathways for *D. russelii* towards low plains.

observed distribution and suitable climate spaces that can ease the dispersion (Chowdhury et al. 2022). These findings suggest a strong influence of climate and biophysical factors on this snake's expansion.

In addition to inhabiting favourable climate spaces, *D. russelii* will find suitable cropland habitat, especially paddy fields in agrarian Bangladesh. The recent increasing cultivation of paddy fields in Bangladesh, to meet the demand for this staple food for the vast human population of the country (Jalilov et al. 2019), provides favourable habitats for *D. russelii*. The introduction of hybrid rice varieties and improved irrigation have led to multiple rounds of rice cultivation throughout the year (Tiongco and Hossain 2019), enhancing the habitat suitability for this viper by providing abundant prey and shelter (Wüster 1998), as well as camouflaged hiding places for escaping predators (Móré et al. 2024), and suitable conditions for daily activities (Glaudas 2021). Small mammals such as rodents, crabs, frogs, and birds are significant food sources for adult and juvenile *D. russelii* (Wüster 1998; Rahman 2015; Khan 2018). The availability of prey is directly correlated with the healthy body and reproductive success of snake species (Brown et al. 2017). In addition, reduced predator and competitor populations may further support the population expansion of this species, leading to a higher prevalence in the country. In combination, widely suitable climatic conditions (Chowdhury et al. 2022), anthropogenic land use changes (Webb and Shine 1997), and increased availability of prey (Bonnet et al. 1999) are likely to be strongly positive influential factors for the occurrence of this viper in large parts of Bangladesh, and for its dispersal into previously unoccupied localities.

We assume that males and females have equal exposure and likelihood of being found by humans. However, among our field-collected *D. russelii* from 2019 to 2021, we observed an increase in the proportion of females, suggesting a potential female-biased population structure for this viper in Bangladesh. A female-dominant population, along with the species' ovoviviparous mode of reproduction, high fertility rate, and large clutch sizes (6–63 live offspring), might also facilitate rapid population growth (Daniel 2002). Moreover, it is tempting to speculate whether increasing temperatures in Bangladesh over recent decades (Rahman and Lateh 2016) might have favoured the production of female offspring through temperature-dependent sex determination (Bull 1980) since temperature thresholds during

the incubation period can lead to the development of either male or female offspring in reptiles including snakes (Charnier 1966). Whether or not this plays a role in *D. russelii* warrants further scientific investigation.

While this viper species benefits from currently available climate spaces in Bangladesh, projected climate changes for the future may reduce suitable climate spaces, particularly in northwestern and central regions of the country. Temperature and precipitation emerged as significant factors in shaping suitable climate space for snake species (Wu 2016; Chowdhury et al. 2021, 2022), and this is also observed here for *D. russelii*. As poikilothermic animals, the physiological processes of snakes, such as reproduction and metabolism (Teixeira and Arntzen 2002), are influenced by ambient temperature and precipitation (Aubret and Shine 2010). We found that the temperatures of the cold season and precipitation in the dry season positively influence the distribution of *D. russelii* in Bangladesh, while seasonal temperature fluctuations and lower annual precipitation negatively impact its distribution. In the face of rapidly advancing climate change, these factors could contribute to the decline of suitable climate spaces for this species in the future.

As *D. russelii* is a highly dangerous, medically important venomous snake species, its observed geographic range extension, and the likelihood of its presence in, or dispersal to, additional suitable areas of Bangladesh, pose significant public health concerns. These are reflected by increased reports of morbidity and mortality due to envenoming by this species from different locations of Bangladesh (Haidar et al. 2023; Amin et al. 2024). Those reports further suggested that this snake species may have spread to as many as 27 out of the 64 districts in the country. The presence of *D. russelii* in agricultural landscapes and resulting snake-human conflicts (Jaman et al. 2020) also causes fear among farmers (Rahman et al. 2010). On the other hand, lack of awareness of the presence of this highly venomous snake can lead to insufficient preventive practice and allocation of healthcare resources for the management of *D. russelii* envenoming. Our research identifies additional areas of Bangladesh where this species is likely to occur, and field workers and farmers as well as public health and healthcare professionals in these areas should be informed about the possible presence of this viper and recommended preventive practice. Public awareness campaigns and wearing protective gear during agricultural work are critical to mitigate risks. Victims must be educated to prioritize seeking modern healthcare facilities for effective treatment. We recommend that health policymakers consider the directional trends in the expansion of this venomous snake to implement preventive measures and allocate resources effectively to enhance public health safety.

At the same time, human-snake conflict in a country with a high human population density is a limiting factor for the dispersal of snakes (Glaudas 2021). The fearful and aggressive attitude towards snakes (Jaman et al. 2020) often results in snake killings which may lead to unnoticed declines of their populations. In the face of this, the projected reduction of future suitable climate spaces for this species in Bangladesh should raise concern for conservationists. While it is imperative to urgently implement measures to minimise fatalities caused by this species, through effective snakebite management emphasizing public awareness, mitigating snake-human conflicts, improving preventive practices and provision of healthcare for snakebite patients especially in rural areas, developing efficacious policies to ensure the sustainable survivability of *D. russelii* in the future is also very important.

In recognising the limitations of this research, we suggest that incorporating a broader range of ecological, climatic, and anthropogenic factors could enhance our understanding of the rapid expansion of venomous species. A longer-term field study beyond the four years of observation and collection could provide more precise insights into the dispersal patterns and sex ratio of this viper. Although we assumed equal capture probability for male and female vipers, further research on the capture efficiency of male and female *D. russelii* would provide a more accurate assessment of the true male-to-female ratio in the wild population. Such comprehensive analyses are crucial not only for effective conservation and public health management in Bangladesh but also for addressing similar challenges posed by venomous species globally, particularly in regions experiencing parallel ecological and climatic shifts.

Conclusion

The highly venomous *D. russelii*, one of the world's most medically important viper species, has a much larger geographic distribution in Bangladesh than previously documented and it appears to be expanding its population and range into new areas of this country. We explained the climatic and environmental factors, with high cold-season temperatures and dry-season precipitation as well as human land-use changes creating optimal habitats for this snake. As the observed distribution of this species so far covers only a portion of the climatically suitable spaces in Bangladesh, it is expected to already occur in certain additional regions and/or to be able to disperse to these in the near future. The snake's strong swimming capability allows it to utilise river currents for range expansion particularly during the monsoon season, with temporary floodplains subsequently becoming viable dry-season habitats. Terrestrial dispersal is facilitated by the absence of physical barriers, and newly occupied habitats often feature croplands and grassy vegetation, offering abundant prey and minimal predators. However, projections indicate a shrinking of climatically suitable habitats in the future due to seasonal temperature variability and reduced precipitation. As the medical relevance of *D. russelii* and associated human-wildlife conflict also lead to the targeted killing of snakes, this ecologically and economically important predator of rodents is also exposed to significant

anthropogenic threats. Proactive management strategies must mitigate the impacts of snakebite to prevent mortality and morbidity of the envenoming bite of this viper.

Acknowledgements

We are grateful to all members of the Eco-climate Lab, Department of Zoology, University of Chittagong, Chattogram, Bangladesh, for their help during this research. We are also thankful to Borhan Biswas Romon, Md. Sahidul Islam, Mohammad Shahjahan, and Sharif Rajon for their co-operation during fieldwork and responding to rescue call. We extend our gratitude also to the Venom Research Centre, Bangladesh, for providing Russell's viper data.

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Supplementary material 1

The Seven spatial variables and their categories used for the current analysis

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Data type: docx

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Link: https://doi.org/10.3897/herpetozoa.38.e143411.suppl1

Supplementary material 2

ODMAP document

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Data type: csv

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Link: https://doi.org/10.3897/herpetozoa.38.e143411.suppl2

Supplementary material 3

Predators of *Daboia russelii* in Bangladesh

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Link: https://doi.org/10.3897/herpetozoa.38.e143411.suppl3

Supplementary material 4

Competitors of *Daboia russelii* in Bangladesh

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Data type: docx

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Supplementary material 5

Predicted suitable climate for *Daboia russelii* in current and future (2080) climate scenario

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Data type: docx

Explanation note: Suitable climate map of Daboia russelii in Bangladesh. Present and future (2080) suitable climate Space predicted by Bioclim and Maximum Entropy (Maxent) Model.

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Link: https://doi.org/10.3897/herpetozoa.38.e143411.suppl5